

The I Gene and Broad Spectrum Potyvirus Resistance

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Hypersensitivity to five viruses of the common bean has been attributed to dominant alleles at loci designated I (bean common mosaic virus, BCMV), Bcm (blackeye cowpea mosaic virus, BICMV), Cam (cowpea aphid-borne mosaic virus, CAbMV), Hss (soybean mosaic virus, SMV) and Hsw (watermelon mosaic virus-2, WMV-2) (Provvidenti, 1987). These pathogens are distinct, but clearly related members of the largest and most devastating family of plant viruses, the potyvirus group, named for the type member, potato virus Y. At least 14 of the >100 group members can be transmitted to bean mechanically and non-persistently by aphid spp., and several are seed-transmitted with high frequency.

Dominant host genotypes show complete local and systemic resistance to most pathotypes of BCMV, and all isolates of BICMV, CAbMV, and WMV-2 tested at <30C. However, at higher temperatures, e.g. >33C, a very distinctive necrotic response rapidly develops after inoculation. A similar reaction occurs independent of temperature with SMV isolates or BCMV pathotypes NL-3, NL-5 and NL-8 (Drijfhout, 1978). Initially, pinpoint lesions or small dark necrotic flecks appear on inoculated leaves within 2-5 days. Necrosis can spread systemically through the vascular tissue resulting in dark stem streaks and apical death. Early histological studies of this condition, termed "black root," confirmed that phloem death resulted from systemic spread of bean common mosaic virus in these genotypes (Grogan and Walker, 1948; Jenkins, 1941). Because of the importance of BCMV worldwide, the I gene (Ali, 1950) has been backcrossed into most advanced breeding lines and commercial varieties to eliminate seed transmission and losses to mosaic disease. However, the recent development and spread of "necrotic" BCMV pathotypes which incite rapid death of II lines under field conditions in Africa, the Midwest, and the Caribbean basin has called this strategy into question.

Preliminary observations of diverse bean germplasm indicated that this very distinctive necrotic response was incited by all five potyviruses. Further, it was dominant in each case and occurred only on I-genotypes. Based on this correlation, and the similarity of phenotype and inheritance, a study of the genetic relationship among these factors was undertaken (Kyle, 1988). First, no recombinant families were identified when sets of >12 seedlings from >1,000 (BT-2 x BT-1) F₃ families were inoculated separately with each virus. From these data, the maximum recombination frequency between the most distant pair of factors, if they are distinct, was estimated to be <0.0023 at 99% confidence probability. Second, diverse types of varieties, experimental lines and plant introductions were screened with each virus. All hypersensitive BCMV-resistant lines developed a similar response to the other viruses. No BCMV-susceptible lines were hypersensitive to any of the viruses. Third, the BCMV-resistant variety, Corbett Refugee (CR), developed in 1931 by Ralph Corbett from a spontaneous mutant at the I locus (Pierce, 1934), was obtained from several sources and increased from single seeds. The original resistant individual was identified in cv. Stringless Green Refugee, which was also obtained from several sources and

confirmed to be uniformly susceptible. All CR lines did not develop mosaic upon inoculation with any of the viruses. To establish whether resistance was both dominant and associated with the mutation at the *I* locus, CR was crossed with the unrelated *II* line, BT-1. The F_1 , with independent sources of the mutation at *I* in trans, was testcrossed to a uniformly susceptible line, BT-2. Progeny were inoculated with each of the five viruses at 35°C. All plants inoculated with BCMV developed systemic vascular necrosis, as expected. Further, no segregation was observed for hypersensitivity to the other four viruses. The only factor(s) for resistance to these viruses in BT-1 are at or closely linked to the *I* locus. Because these testcross progenies were all uniformly hypersensitive to the five viruses, either separate, tightly linked mutations for phenotypically identical, dominant potyvirus resistance, or the spontaneous mutation at *I*, determined reactions to the five viruses in Corbett Refugee.

Finally, lines which carry factors epistatic to the *I* allele and therefore show modified or suppressed necrosis upon infection with BCMV, e.g. *I*⁻ lines that are homozygous recessive at *bc-u* and *bc-1*, *bc-2* or *bc-3*, were evaluated with each of the five viruses at 25°C and 35°C. Striking phenotypic similarity of responses was observed in extremely diverse genetic backgrounds including the complete set of BCMV host differentials. Thus, genes which altered or suppressed expression of the *I* allele with BCMV in the lines tested, similarly altered or suppressed reaction to the other four potyviruses. If there are distinct factors for hypersensitivity to these viruses, they are not only tightly linked and phenotypically indistinguishable, but also subject to extremely similar epistatic interactions. Virus culture purity was monitored by immunodiffusion, ELISA, host indexing and characteristic symptomatology on a variety of susceptible species and genotypes. Taken together, these results do not prove but are most consistent with the hypothesis that a single allele at the *I* locus confers temperature-dependent resistance to four clearly distinct but related potyviruses, BCMV, BICMV, CABMV, WMV-2 and temperature-independent hypersensitivity to a fifth potyvirus, SMV. The possibility of five tightly linked distinct loci or two or more dominant pseudoalleles at a complex locus cannot be conclusively ruled out with Mendelian genetics. Regardless of the fine structure at the *I* locus, these studies clearly demonstrate the phenomenon of simply inherited broad spectrum plant virus resistance.

References

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